

BIOTIC DIVERSIFICATION IN THE PHANEROZOIC: DIVERSITY INDEPENDENCE

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ABSTRACT. The concept of global taxonomic diversity tending to an equilibrium state is central to many macroevolutionary hypotheses. It is widely accepted and considered to be corroborated by quantitative models of biotic diversification in the Phanerozoic. Those models assume diversity dependence of the rates of extinction and origination of taxa. This basic assumption, however, is contradicted by the empirical data. The process of diversification may depend on historical contingencies rather than on general macroevolutionary laws.

THE pattern and process of biotic diversification in the Phanerozoic have been subject to a heated controversy over the last dozen years or so. Rival hypotheses on biotic diversification propose that it is either controlled by extrinsic factors (Valentine 1973), or continues practically limitless (Whittaker 1977), or tends to an equilibrium diversity set by the limits to specialization and to decrease in the average population size (Levinton 1979). A consensus seems to have developed recently that the last hypothesis holds true. In the absence of direct evidence the hypothesis is widely considered to be corroborated by quantitative models of diversification which customarily assume diversity dependence of the rates of origination and extinction of taxa (Sepkoski 1978, 1979; Carr and Kitchell 1980; Kitchell and Carr 1985). These rates are expected to change conversely, or at least to converge, with increasing diversity. Given absence of significant perturbations this would lead to a global equilibrium in diversity. This concept has been central to much macroevolutionary research (Raup *et al.* 1973; Gould *et al.* 1977; Schopf 1979*a*) and it underlies many macroevolutionary hypotheses (Schopf 1974; Simberloff 1974; Bambach 1983; Sepkoski and Sheehan 1983).

The consensus on equilibrium diversity, however, is unwarranted. The models of biotic diversification have not been adequately tested. There are in fact no good empirical data to test any models of evolution of global diversity. Theoretical justifications for those models refer to the species level of the taxonomic hierarchy. Reliable data on global species diversity in the Phanerozoic are beyond the resolution potential of palaeontology, however, at least at the present state of knowledge. Therefore, family level data are widely accepted as the best approximation and customarily applied to macroevolutionary analyses of global diversity.

In the present study I use such data to test the basic assumption of most models of biotic diversification, i.e. the assumption of diversity dependence of taxonomic evolutionary rates. If this assumption is not met, the apparent fit of the models' predictions to the empirical pattern is virtually meaningless.

DATA AND RESULTS

In spite of criticisms (Raup 1972, 1976; Sepkoski 1976; Signor 1978) pointing to severe biases inherent in an early compilation of global diversity in the fossil record (Valentine 1969), an essentially similar compilation by Sepkoski (1982) is widely used as the empirical pattern of taxonomic diversity during the Phanerozoic (Raup and Sepkoski 1982, 1984; Sepkoski and Sheehan 1983; Van Valen 1984; Kitchell and Carr 1985). This is commonly substantiated by the intercorrelation of a number of estimates of fossil diversity which remains significant even after the removal of the effect of their correlation to geological time, and thus demonstrates the reality of the underlying pattern (Sepkoski *et al.* 1981). Correlation analysis, however, cannot indicate which one of the analysed estimates is the most accurate. Yet they widely differ in many important aspects including the presence or absence of a Palaeozoic plateau in diversity. More importantly the correlation analysis was carried out at the

system level of stratigraphic resolution and hence cannot substantiate a pattern at the stage level. Finally, a more recent analysis of inherent sampling biases in that data set shows that their quantitative effects may approach an order of magnitude (Signor 1982). Much caution is therefore necessary in any quantitative inference from those data.

Nevertheless, I use Sepkoski's (1982) compilation as a source of data on global family diversity and the rates of family extinction and origination during the Phanerozoic because (i) this is the empirical pattern that diversity curves predicted by the theoretical models were tested against, and (ii) no better set of data on global taxonomic diversity is available. I computed the average family diversity and the probabilistic rates of family origination and extinction for each of the post-Tommotian stratigraphic stages listed in Sepkoski's compilation. Rate of origination was calculated as the number of originations in a stage divided by the number of families extant at the end of the preceding stage. Rate of extinction was computed as the number of extinctions in a stage divided by the number of families that survived from the preceding stage plus all those that originated in the given stage. This procedure assumes that all originations and extinctions were clustered at the beginning and the end of each stage, respectively, but it overcomes the bias of erroneous estimates of the absolute duration of particular stages; analytical error in absolute age determination of stratigraphic boundaries increases significantly with geological age and may exceed stage duration considerably (Odin 1982; Harland *et al.* 1983). Records with stratigraphic resolution at the level of series or system were assigned to the component stages proportionately. Only a negligible minority of the total number of families have stratigraphic ranges shorter than a stage, which attests to appropriateness of the time scale (Mark and Flessa 1977).

Based on this data set, there is a highly significant ($P < 0.01$) correlation between family diversity and the rates of family origination ($r = -0.594$) and extinction ($r = -0.630$) over the seventy-six post-Tommotian stages. This may be artificial, however, for there is a strong correlation between geological time and both taxonomic diversity and taxonomic evolutionary rates at the family level. Family diversity significantly increases (Valentine 1969; Sepkoski *et al.* 1981; Signor 1982), while the rate of family extinction significantly declines through time (Raup and Sepkoski 1982; Van Valen 1984). Spurious correlations may also arise because (i) the analysis involves time series, and (ii) the probabilistic rates of extinction and origination are by definition related to diversity as they contain its measure in the denominator. The data set was therefore subdivided into four time intervals separated by the major extinction events (Ashgillian, Guadalupian-Dzhulfian, Maastrichtian): early Cambrian to late Ordovician, early Silurian to late Permian, early Triassic to late Cretaceous, and early Tertiary to Quaternary. The mass extinctions, however, were not excluded from the analysis because there is no compelling evidence to support their interpretation as outliers (Quinn 1983; Raup *et al.* 1983).

Correlation coefficients between diversity and rates of origination and extinction for each time interval are given in Table 1. Except for the rate of origination in the later Palaeozoic, none of these correlations is significant at $P = 0.05$; the correlation of the later Palaeozoic rate of family origination to diversity is nonsignificant at $P = 0.02$. Exclusion of the mass extinctions improves the correlations in the later Palaeozoic only. Generally, the correlations do not attain significance over still shorter time intervals. This rules out the possibility that the time scale is too crude to account for changes in the relationship of extinction and origination rates to diversity (Hoffman and Kitchell 1984). Introduction of one-stage time lag between diversity and the rates of origination and extinction does not improve the correlations.

Choice of the level of statistical significance to be regarded as biologically meaningful is always arbitrary, and it might be argued that even $P = 0.1$ would not be too liberal a level given the biases inherent in the fossil record. Many correlation coefficients given in Table 1 are significant at that level, but they are all negative which contradicts the concept of converse dependence of the rates of origination and extinction on diversity. The taxonomic evolutionary rates still might converge with increasing diversity. For none of the time intervals, however, is the difference between slopes of the respective regressions significant.

DISCUSSION

This analysis shows the absence of significant correlation between the global taxonomic diversity and taxonomic evolutionary rates. It is crucial to emphasize that the null hypothesis tested in this study predicted the occurrence of such a correlation. The fact that spurious correlations might be expected to arise in the analysed system makes the evidence for rejection of the null hypothesis even more compelling.

It might be argued that the absence of significant correlations is due to the lumping of what Sepkoski (1981; see also Sepkoski and Sheehan 1983) recognized as three consecutive evolutionary faunas into a single biotic system in the present analysis. If two or more distinct groups of taxa, which

partly overlap in time, each exhibit their own diversity-dependent extinction and origination rates, there may be no correlation between the total taxonomic evolutionary rates and total diversity as computed for the global biota. The validity of Sepkoski's (1981) factor analytic description of the fossil record is questionable, however, because there is no evidence to support the claim that the evolutionary faunas are anything more than abstract statistical constructs (Hoffman, in press; see also discussion on the reification of factor analytic solutions by Gould 1981). Even if the lack of correlations were the result of lumping Sepkoski's (1981) faunas, this could account for the absence of diversity dependence from the Cambrian to Ordovician only, which indeed covers two distinct faunas. The Silurian to Permian interval, however, covers essentially the Palaeozoic fauna of Sepkoski (1981), with the modern fauna largely congruent in pattern and the Cambrian fauna negligible; the Mesozoic and Cenozoic time intervals, in turn, cover almost exclusively the modern fauna of Sepkoski (1981). Thus, there is no evidence for diversity dependence in the evolutionary behaviour of the alleged faunas either. This result contradicts the assumption that diversity dependence of the rates of family origination and extinction leads to a global equilibrium in diversity. It refutes the macroevolutionary models of biotic diversification based on the logistic equation.

This conclusion does not necessarily imply that the taxonomic diversity of the biosphere increases indefinitely, nor even that its upper limits are set entirely by abiotic resources. First, the data analysed here may be too biased to allow a reliable inference. Secondly, the level of taxonomic resolution may be inadequate if (i) the family is merely a taxonomic artifact with its biological meaning widely variable among organic groups, or (ii) the family/species relationship is widely variable through geological time (due merely to the taxonomic structure we impose on the biota or to the very nature of the evolutionary process; Raup 1983; Flessa and Jablonski, in press). In this case family diversity is meaningless as a measure of biosphere proximity to the limits to specialization and decrease in the average population size and there may be no congruence between the patterns at the family and the species levels. Thirdly, regardless of the existence or not of biotic limits to global diversity, the actual diversity may be primarily controlled by abiotic (Valentine 1973) or biogeographical (Valentine *et al.* 1978; Schopf 1979*b*; Wise and Schopf 1981) factors. Fourthly, the concept of the biosphere responding predictably (even though under a weak, statistical definition of determinism) to perturbations may be wrong, for taxa may not be validly considered as indistinguishable particles (Hoffman 1981, 1983). Identical perturbations may prompt widely variable biotic responses

TABLE 1. Correlation coefficients between taxonomic evolutionary rates and diversity.

Time interval	Number of stages	Rate	Correlation to diversity r
Atdabanian to Ashgillian	14	origination	-0.365*
Llandoveryan to Dzhulfian	21	extinction	-0.304*
Induan to Maastrichtian	29	origination	-0.458
Danian to Pleistocene	12	extinction	-0.351*
		origination	-0.322*
		extinction	-0.097*
		origination	-0.512*
		extinction	-0.359*

* Asterisks denote correlations not significant at $P = 0.05$.

depending on particular configurations of the biosphere (taxonomic composition, biogeographical structure, etc.). The rates of origination and extinction of taxa may depend primarily on historical contingencies rather than on general laws. The last possibility might account for the observed lack of order but also for the absence of strict randomness (Flessa and Levinton 1975) in the evolution of biotic diversity.

The hypothesis of global equilibrium in species number as the upper limit to the process of biotic diversification is thus compatible with, though not supported by, the empirical data on family diversity, extinction, and origination. They contradict, however, the alleged evidence for its correctness, derived from the apparent fit of the curves predicted by macroevolutionary models of diversification to the empirical pattern. There is no other conclusive evidence to support this hypothesis.

The present results are irrelevant to the hypothesis of regional or continental evolutionary equilibrium as derived from the theory of island biogeography (Rosenzweig 1975; cf. Hoffman, in press). The latter concerns the species level of the taxonomic hierarchy and a much finer time scale.

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